

## CHEMICAL ATTRACTION CAUSING AGGREGATION IN THE SPINY LOBSTER, *PANULIRUS INTERRUPTUS* (RANDALL), AND ITS PROBABLE ECOLOGICAL SIGNIFICANCE

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### ABSTRACT

Field and laboratory experiments were performed to determine the mechanisms of aggregation by the lobster, *Panulirus interruptus*. Capture-frequencies by unbaited traps, modified to simulate refuges by allowing lobsters to both enter and exit, were found to fit a negative binomial ( $k < 0.5$ ) rather than a Poisson distribution. Such over-dispersion in the capture of lobsters was not fully attributable to environmental factors, suggesting that conspecific attraction may have been occurring. Laboratory trials conducted in a large rectangular tank (9.0 m  $\times$  2.4 m  $\times$  1.0 m) demonstrated that substances released by both sexes are highly attractive to conspecific males and females alike, resulting in aggregation. Abalone muscle, a potent feeding attractant to *P. interruptus*, was ineffective in initiating aggregation while dead lobsters, excised lobster thorax and abdominal muscle were all avoided. The tendency to aggregate changes during the course of a night, and aggregations are probably formed just before dawn and maintained until dusk. Results are consistent with a hypothesis that conspecific interactions facilitate anti-predatory defense and avoidance in *Panulirus*.

### INTRODUCTION

Benefits of living in groups include a reduction in predation by concealment among cohorts (Williams, 1964; Hamilton, 1971), collectively increased prey vigilance (Pulliam, 1973; Treisman, 1975a, b), cooperative foraging (Schoener, 1971), increased reproductive success (Alexander, 1974), and competition leading to increased foraging efficiency (Pulliam, 1976). However, aggregation does not always imply benefit, or that gregarious behavior has occurred. Habitat patchiness and lack of refuges can also cause contagious spatial distributions.

The discovery of aggregation-causing attractions between individuals would give evidence for gregariousness. Although chemical signals are known to mediate social behavior in both terrestrial and aquatic arthropods, most previous investigations have emphasized those which lead to courtship and mating, that is sex pheromones (see Jacobson, 1972, and Dunham, 1978, for reviews). Other studies have reported colonization effects, as in beetles (*e.g.*, Wood, 1962; Birch, 1978; Borden, 1982, 1984) and in barnacles (*e.g.*, Crisp and Meadows, 1962; Rittschof *et al.*, 1984), in which chemical attraction has led to high conspecific densities in habitats that enhance survival. Chemical cues have also been found to specifically mediate group foraging activities, as in the exploratory trails by ants (*e.g.*, Wilson, 1962; Holldobler and Wilson, 1970; Holldobler, 1977; Ritter *et al.*, 1977; Williams *et al.*, 1981) and termites (Stuart, 1970).

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Several species of eusocial insects release an alarm pheromone upon attack by predators to enhance aggregation and aggressive behaviors toward the intruder (e.g., Wilson, 1971; Longhurst *et al.*, 1979; LaMon and Topoff, 1981; Howse, 1984). As far as we know, however, there is only one example in the chemoreception literature of anti-predatory defensive grouping prior to predator detection. In this example, both sexes of the beetle, *Lycus loripes*, were found to aggregate by means of chemical emission from the males (Eisner and Kaftos, 1962). Since *Lycus* releases an offensive odor when attacked, group living presumably aids the individual by reinforcing avoidance behavior in predators.

The present study provides data on chemical attraction leading to the formation of aggregations in a marine decapod crustacean, *Panulirus interruptus* (Randall). Field and laboratory studies have shown that the California spiny lobster forages at night and resides in shelters during daylight hours either alone or in groups (Lindberg, 1955; Roth, 1972). In contrast to the clawed lobsters of the family Nephropidae (Atema and Cobb, 1980), communal den occupancy and aggregation behavior occurs throughout the family Palinuridae (Lindberg, 1955; Fielder, 1965a; Berry, 1971; Berrill, 1975, 1976; Herrnkind *et al.*, 1975; Cobb, 1981), though its mechanism has previously been undetermined. Shelter selection by one individual followed by chemically mediated, conspecific attraction could lead to the formation of these aggregations. In this study, we establish that substances released by spiny lobsters attract conspecifics to shelters. Further evidence shows that both chemical release and attraction are not sex specific and that shelters containing dead conspecifics are avoided. The observed chemical attraction is assigned an anti-predatory function.

## MATERIALS AND METHODS

### *Field experiments*

Field trapping experiments were performed to provide correlative information concerning the formation of aggregations by *Panulirus interruptus*. It was the purpose of these experiments to provide capture-frequency data for comparison to theoretical Poisson and negative binomial distributions. The Poisson distribution has been used to test for randomness and independence among captures (Sokol and Rohlf, 1981), while the exponent,  $k$ , of the negative binomial distribution measures over-dispersion and aggregation (Taylor *et al.*, 1979). A value of  $k$  approaching infinity occurs when capture is random, while  $k$  approaches zero as capture becomes increasingly contagious. An iterative process was used in estimating  $k$  (Bliss and Fisher, 1953).

A 50 m  $\times$  100 m quadrat was established in December, 1978, approximately 150 m offshore in 4–7 m depth over a rocky reef in the More Mesa coastal area of Santa Barbara, California. Unbaited traps, modified to allow both entrance and exit, were placed to simulate heretofore uncolonized shelters. Trap selection by a founding lobster appeared to be based primarily on thigmotaxis. Traps were positioned in a 2  $\times$  4 matrix with adjacent traps separated by 25 m. Traps were set at 0800–1000 h and pulled after 24 h on 10 occasions. Replicate experiments were performed during June, 1979, and again in July, 1980. In these later tests, unbaited traps were positioned at 16 permanently buoyed stations that were located slightly inshore (2–4 m depth) of the quadrat area. All captured animals were tagged before release (Zimmer-Faust and Case, 1982), but no recaptures occurred during these experiments.

### *Laboratory experiments*

*Collection and maintenance of animals.* Lobsters of 65–102 mm carapace length were captured by trapping or by hand (SCUBA) at More Mesa reef and brought

immediately to laboratory holding tanks (1.2 m diameter  $\times$  0.6 m depth). Animals were maintained in tanks for two weeks prior to experimentation, with aeration and ambient sea temperature (15–18°C) maintained by a constant seawater flow. A 12:12 D:L (light on: 0800 h) cycle was imposed, starting at least 7 days before tests. Animals were fed mackerel on alternate days and tanks were drained and thoroughly rinsed after each feeding to ensure that residual food odors did not contribute to responses in subsequent experiments.

*Test tank.* All tests were performed in a large, rectangular fiberglass tank (9.0 m  $\times$  2.4 m  $\times$  1.0 m). Seawater entered at one end of the tank through regularly spaced holes in a horizontally positioned pipe, and flow (28 ml  $\cdot$  cm<sup>-2</sup>  $\cdot$  min<sup>-1</sup>) was rendered semi-uniform by a vertically aligned plexiglass baffle system and a horizontal stack of 0.6 m  $\times$  1.3 cm PVC pipes. Outflow was established by two 7.2 cm diameter PVC stand pipes symmetrically positioned at the downstream end of the tank so as to maintain a constant water depth of 45 cm. Plexiglass observation windows positioned in the tank along the sides and bottom enabled direct observation of lobster behavior. To assist traction of walking animals, bottom windows were covered with 0.6 cm mesh vexar, and artificial substratum was attached to the bottom surface. A rectangular 0.5 m  $\times$  1.0 m PVC sheet was suspended horizontally over the most downstream observational window, to provide a starting point for test animals. Lobsters readily congregated under this overhang when they were introduced during daylight hours, 6 h prior to the initiation of experiments.

*Use of traps as shelters.* Elliptically shaped (100 cm length  $\times$  79 cm width  $\times$  30.5 cm height) polyethylene mesh traps (Fathoms Plus Co., San Diego, CA) were used as shelters in these experiments. We considered the traps to provide an adequate shelter stimulus because (1) lobsters readily entered and left traps in laboratory experiments, following modification of trap entrances to produce shallow slope and height (15 cm), and (2) unbaited traps often captured lobsters in field experiments (Zimmer-Faust and Case, 1982, 1983). Trap residencies by lobsters were maintained by choice in the present experiments.

*General procedures.* Two traps (shelters) were paired side by side, 4.0 m upstream from the PVC overhang. A stimulus was added to one but not to the other trap, to test for its influence on inherent trap attraction. Additional trials were later used to evaluate the relative influences of two competing stimuli, by placing each in opposing traps.

For each test four lobsters were put in the test tank at 1400 h and immediately took up residency under the PVC overhang. The selection of lobsters for each test was at random, except that each was subjected only once to a given stimulus. Stimuli were introduced into traps at 1945 h, just 15 min prior to the onset of the night phase. Final residency patterns were recorded the following morning at first light (0800 h), since observations showed that each lobster retained its residency throughout the day (0800–2000 h). Periodically, we recorded patterns of shelter occupancy during the night to determine when animals first left the PVC overhang area and when they first took up residency in traps. Movement of animals from one trap to the other was assessed by watching marked animals through plexiglass windows using dim red illumination.

We limited experiments to the months of June–December, 1982–1984, to avoid possible complications from reproductive activity. Mating occurs in *P. interruptus* during the January–May interval (Mitchell *et al.*, 1969). Only hard-shelled lobsters were used, and females carrying eggs or spermatophores were excluded.

*Experiment A: responses of lobsters to conspecific odors.* Tests were first performed to determine whether *Pamulirus interruptus* releases substances which attract conspe-

cifics. Either four male or four female lobsters were used as test animals during each trial, and a stimulus animal, either male or female, was isolated in one of two opaque headtanks (30 × 30 × 20 cm) positioned 0.5 m above the test tank. The opacity of the headtanks ensured that visual contact was not made between stimulus and test animals. Continuously flowing seawater was conducted from one headtank (3.0 l/min) to the center of one of the traps, while the opposing headtank conducted seawater into the alternative trap. Both stimulus and test animals were replaced and the position of the stimulus animal was reversed with each successive trial.

*Experiment B: responses of lobsters to living and dead conspecifics, living and dead crabs, and prey tissues.* Additional tests were performed to determine whether any conspecific attraction in the first experiment resulted from foraging or shelter-related gregarious activities. Attraction of lobsters to carrion placed in shelters was used to assay the possibility that foraging caused aggregations, while attraction only to live conspecifics and not to carrion was taken to indicate that shelter-related behavior was gregarious in nature. We used only male animals in these experiments due to time constraints, and because male and female test animals responded nearly identically to odors presented in the first experiment (see Results, Table II).

Abalone (*Haliotis* spp.) muscle was used as a carrion stimulus, because of its preferred status as food to *P. interruptus* (Carlberg, 1975) and because of its proven ability to attract lobsters in field trapping experiments (Zimmer-Faust and Case, 1982, 1983). Carrions derived from killed lobsters and crabs (*Cancer antennarius*) and from lobster thoraces and abdominal muscle tissues were also tested. Animals were killed just prior (<5 min) to their use in experiments by crushing between the eyestalks after which a dorsal incision was made laterally between the thorax and the tail to expose underlying tissues. Alternatively, some animals were killed for tests by holding on dry ice for 10 minutes. This latter procedure minimized damage to the exoskeleton, while the former maximized release of body and tissue fluids.

In each trial, either carrion or a live animal was placed in a cylindrical, 6-mm mesh vexar container and attached to the center bottom of one trap. The container allowed odor release, while preventing contact between its contents and test animals. An identical empty container in the opposing trap controlled for container volume and surface. Headtanks were not used in these tests, to minimize the dilution of potential feeding attractants. Owing to their fragility, lobster abdominal muscle and abalone muscle (100 g wet tissue) were protected from physical dispersion by being placed in 3-mm mesh vexar bags before being put in containers.

## RESULTS

### *Qualitative field observations*

Observations were made of aggregations using SCUBA at More Mesa reef, during April, 1979, and again in June, 1980. Dens were abundant along undersides of large boulders which had become undercut and the sand removed by tidal surge, and also among the rubble of collapsed or fractured rocky reef ledges (Fig. 1). As many as 30 or more lobsters occupied a single den while a nearby (<5 m distant) refuge of seemingly equal quality was present and uninhabited. A total of 16 dens having multiple occupancies of both male and female lobsters, approximately 65–90 mm in carapace length, were marked by buoys and monitored for 5 consecutive days. No attempt was made to tag individuals or to follow the residency patterns of individuals, since such disturbances could have adversely affected communal behavior. Of the total, eight dens had multiple occupancies on each day. The remaining eight dens exhibited a variety

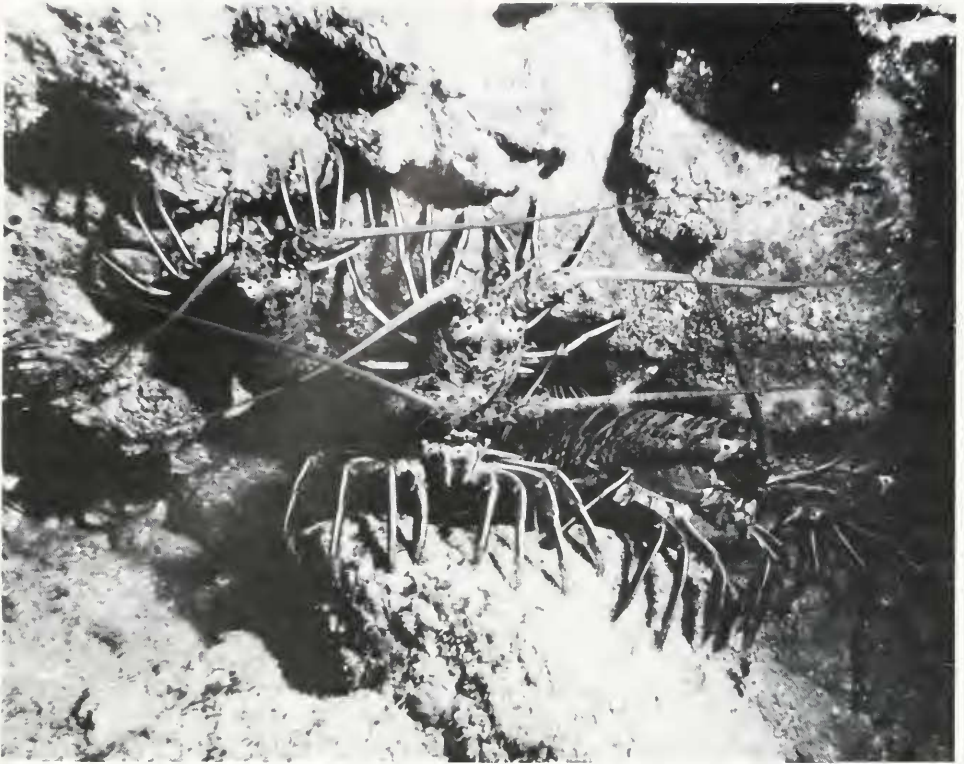


FIGURE 1. Natural habitat of *Panulirus interruptus* showing a den occupied by five animals at More Mesa reef. Though physical characteristics of dens vary considerably, most are typified by having at least two entrances. One entrance is usually large and open, as seen here, and lobsters orient themselves so that their antennae point outwards. The second entrance is generally much smaller and it is often situated to the rear, where it is used by lobsters to escape if a large predator should penetrate from the front. Lobsters in this photograph are of 65–75 mm carapace length. Photograph courtesy of J. R. McCullagh, Marine Science Institute, U. C. Santa Barbara.

of residency patterns, with occupancies occurring over 1–3 day intervals. Dives both by night and by day in April, 1979, revealed that lobsters did not reside in dens at night, even though they did during the day. Our observations show that aggregations of lobsters are naturally associated with shelters and that both emigration and re-colonization occur on a nightly basis.

#### *Field experiments*

Distributions of lobsters captured in unbaited traps differed significantly from those expected by Poisson distributions (Table 1 and Chi-square Goodness-of-Fit Tests, Expt. 1:  $\chi^2 = 31.76$ , d.f. = 3,  $P < 0.001$ ; Expt. 2:  $\chi^2 = 17.68$ , d.f. = 2,  $P < 0.001$ ; Expt. 3:  $\chi^2 = 5.06$ , d.f. = 2,  $P = 0.07$ ). There was a strong tendency for Poisson models to overestimate captures of single animals, while they underestimated the likelihood of null and of multiple captures, indicating lack of independence between successive capture events. Observed capture frequency distributions were adequately modelled by the negative binomial distribution, with exponent  $k$  assuming values that approached

TABLE I

*Frequency of lobster capture in unbaited traps in field*

Experiment	Number		Size <sup>a</sup> (mm)		Capture frequency			
	Male	Female	$\bar{x} \pm \text{SEM}$	Range	Number (lobsters/ trap · day)	Expected		Observed
						Poisson	Negative binomial <sup>b</sup>	
1 (Dec., 1978)	26	53	69.6 ± 1.2	36-97	0	24.63	46.00	46
					1	29.04	13.93	17
					2	17.04	7.29	9
					3	9.28	4.33	2
					≥4	2.64	8.45	6
2 (May, 1979)	36	34	75.8 ± 1.8	45-121	0	38.82	53.01	53
					1	19.41	4.78	4
					2	4.85	2.18	2
					3	0.81	1.25	2
					≥4	0.11	2.78	3
3 (July, 1980)	7	11	69.7 ± 3.3	46-90	0	64.68	70.00	70
					1	13.75	6.25	7
					2	1.46	2.01	1
					3	1.10	0.82	0
					≥4	0.01	0.92	2

<sup>a</sup> Measured as carapace length.<sup>b</sup> *k* values were 0.408 for Dec., 1978; 0.110 for May, 1979; 0.154 for July, 1980.

zero (Table I and Chi-square Goodness-of-Fit Tests, Expt. 1:  $\chi^2 = 3.04$ , d.f. = 3,  $P > 0.30$ ; Expt. 2:  $\chi^2 = 0.23$ ,  $P > 0.80$ ; Expt. 3:  $\chi^2 = 0.24$ , d.f. = 2,  $P > 0.80$ ). This indicated that capture was highly contagious and over-dispersed. Such over-dispersion was not wholly the result of spatial (trap positioning) or temporal (daily environmental variability) heterogeneity in the probability of capture, since catch was nearly homogeneous at each trap site in all experiments (Chi-square Test-for-Homogeneity:  $P \geq 0.10$ , for each replicate test) and differences in total daily captures were non-significant ( $P > 0.20$ ) except in the first experiment (Chi-square test:  $\chi^2 = 36.62$ , d.f. = 9,  $P < 0.001$ ). These results indicate that factors other than habitat and environmental variabilities are in part responsible for observed capture frequencies, with conspecific attraction a likely factor. There were no apparent differences in size frequencies or sex ratios of animals captured in individual traps, as compared to the total sample captures.

#### *Laboratory experiments*

Field experiments and observations provided only correlative evidence for conspecific attraction, and laboratory experiments were essential to determine the nature of stimuli underlying the formation of aggregations.

*Experiment A.* Both sexes of test animals were found to be significantly attracted to traps (shelters) having conspecific effluence introduced from either isolated male or female stimulus animals (Table II). No preferences were exhibited by either sex of test animal for male or for female effluence, when these stimuli were paired in opposing traps. Results show that both male and female lobsters release chemicals attractive to

TABLE II

*Trap selection by lobsters in the presence of conspecific odors*

Test animal sex	Stimulus		Number of animals residing in traps		Significance <sup>a</sup>	Total number of animals tested
	Test	Alternative	Test	Alternative		
Male	Live male lobster	Empty trap	20	7	$P = 0.047$	32
	Live female lobster	Empty trap	20	8	$P = 0.039$	32
	Live male lobster	Live female lobster	17	13	$P = 0.300$	32
Female	Live female lobster	Empty trap	24	6	$P = 0.016$	32
	Live female lobster	Empty trap	20	6	$P = 0.008$	32
	Live male lobster	Live female lobster	15	13	$P > 0.400$	32

<sup>a</sup> Determined using Wilcoxon Signed Rank Test.

conspecifics and that both males and females possess receptors for, and respond to, attractants. Chemical stimuli were obviously mediating aggregative behavior, even in an absence of visual or tactile cues.

*Experiment B.* Live lobsters were found to attract test animals to traps, as in the previous experiment; however, abalone muscle was unable to affect trap residency (Table III). Control experiments which paired empty traps or paired traps, each with a live lobster, showed no trap biases to exist and no directional preference was exhibited by test animals.

Dead lobsters with crushed carapaces, excised lobster thoraces, and abdominal muscle were all found significantly repellent to test animals (Table IV). Lobsters killed by dry ice were not as repellent, which would be expected if repellency was dependent on the amount of tissue exposed. Dead lobsters failed to modify the attraction of test animals to live lobsters, when these stimuli were paired in opposing traps, and repellency

TABLE III

*Trap selection by lobsters in the presence of live conspecifics and known preferred food*

Stimulus	Stimulus	Number of animals residing in traps		Significance <sup>a</sup>	Total number of animals tested
		Test	Alternative		
Live lobster	Empty trap	50	16	$P = 0.002$	72
Live lobster	Live lobster	16	13	$P > 0.400$	32
Empty trap	Empty trap	15	11	$P > 0.500$	32
Abalone muscle	Empty trap	19	21	$P > 0.500$	40

<sup>a</sup> Determined using Wilcoxon Signed Rank Test.

TABLE IV

*Trap selection by lobsters in the presence of dead conspecifics*

Stimulus		Number of animals residing in traps		Significance <sup>a</sup>	Total number of animals tested
Test	Alternative	Test	Alternative		
Dead lobster <sup>b</sup>	Empty trap	4	20	$P = 0.008$	32
Dead lobster <sup>b</sup>	Live lobster	3	24	$P = 0.008$	32
Dead lobster <sup>c</sup>	Empty trap	8	16	$P > 0.200$	24
Lobster thorax	Empty trap	8	21	$P = 0.047$	32
Lobster muscle	Empty trap	7	22	$P = 0.039$	32
Lobster thorax	Lobster muscle	11	8	$P = 0.500$	32

<sup>a</sup> Determined using Wilcoxon Signed Rank Test.<sup>b</sup> Sacrificed using crushed carapace method.<sup>c</sup> Sacrificed using dry ice method.

was overridden to some extent by a lack of suitable refuge. This last result was demonstrated by pairing lobster thoraces against lobster abdominal muscle, and finding that 60% of all tested animals still chose to reside in traps. Neither living nor dead crabs were found to influence shelter residency by lobsters (Table V).

*Monitoring of shelter residency.* Lobsters moved from beneath the PVC overhang (starting shelter) and began entering traps within 30 min after the onset of darkness (Fig. 2). Marked animals moved freely between traps and residencies were not established during an initial 3.5 h period. Although lobsters did not aggregate in traps during this period, they did by the following morning. This was demonstrated by observing shelter residency patterns at 2330 h and again at 0800 h, for a total of 24 trials (Table VI). Observed data were compared to those values predicted for random assortment by a binomial distribution  $(p + q)^n$ , where exponent  $n$  was the total number of animals residing in traps at each observation time for a given trial, and  $p$  and  $q$  were probabilities of capture for each trap ( $p = q = 0.5$ ). The case where only one animal resided in a trap was not evaluated, because it neither reflected aggregation nor randomness. Differences in values expected for trap residencies at 2330 h and 0800 h were largely a result of different distributions of  $n$ .

TABLE V

*Trap selection by lobsters in the presence of a sympatric crab*

Stimulus		Number of animals residing in traps		Significance <sup>a</sup>	Total number of animals tested
Test	Alternative	Test	Alternative		
Live crab	Empty trap	23	24	$P > 0.500$	56
Live crab	Live lobster	7	22	$P = 0.039$	32
Dead crab <sup>b</sup>	Empty trap	12	12	$P > 0.500$	24
Dead crab <sup>c</sup>	Empty trap	9	7	$P > 0.400$	16

<sup>a</sup> Determined using Wilcoxon Signed Pair Test.<sup>b</sup> Sacrificed using crushed carapace method.<sup>c</sup> Sacrificed using dry ice method.



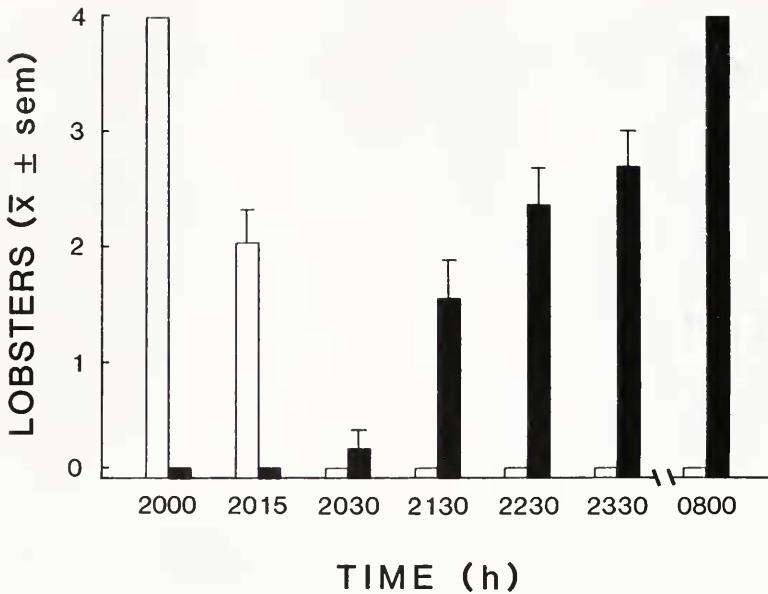


FIGURE 2. Number of lobsters ( $\bar{x} \pm \text{SEM}$ ) residing under the PVC overhang area ( $\square$ ), and the number entering traps ( $\blacksquare$ ) during a 3.5 h observational period following onset of darkness (2000–2330 h) and again the following morning (0800 h). All animals leave the overhang area within 30 min, but not all animals enter traps within the initial 3.5 h period. A total of 10 trials were performed with four animals per trial.

## DISCUSSION

Our results indicate that chemical attraction facilitates conspecific social interactions in the marine crustacean, *Panulirus interruptus*. Specifically, we find that this animal is highly gregarious and that shelter selection influenced by chemical attraction may be the key to explaining the multiple resident denning commonly observed in members of this family. It has been questioned whether communal denning in palinurids is of

TABLE VI

Temporal influence on residency in traps<sup>a</sup>

Time of observation	Assortment in paired traps <sup>b</sup>			Chi-square test		
	$\left\{ \begin{array}{l} 4-0 \\ 3-0 \\ 2-0 \end{array} \right\}$	$\left\{ \begin{array}{l} 3-1 \\ 2-1 \end{array} \right\}$	$\left\{ \begin{array}{l} 2-2 \\ 1-1 \end{array} \right\}$	$\chi^2$ value	d.f.	Sig. ( <i>P</i> )
Night (2330 h)						
Expected by chance	6.88	10.50	4.62	3.81	2	>0.10
Observed	9	6	7			
Day (0800 h)						
Expected by chance	3.00	12.00	9.00	47.19	2	≤0.001
Observed	14	6	4			

<sup>a</sup> n = 24 trials.

<sup>b</sup> See text for explanation.

social origin or is simply a matter of limited availability of shelter (Cobb, 1981). Our results indicate that residency patterns in *P. interruptus* arise in part from non-random habitat colonization and from cohabitation which occurs by choice.

Chemicals mediating cohabitation were not sex specific in either their emission or reception. Because laboratory experiments were performed during non-mating periods, aggregative formation was clearly not associated with reproduction. Abalone muscle, a potent feeding attractant to lobsters, and freshly killed crab both failed to influence shelter selection. Consequently, aggregation formation cannot be attributed to foraging or feeding. This leads us to believe that aggregations are probably anti-predatory in function. It has been observed that group residency in the Western Australian lobster, *Panulirus cygnus*, reduces the penetrability of a den to large mobile predators (Cobb, 1981). We have made similar observations, witnessing *P. interruptus* to position itself so that it points its robust spinose antennae outwards from the burrow (Fig. 1). Cohabiting animals collectively wave their antennae to fend off predatory fishes and divers. The repellency of dead conspecifics would appear to facilitate defense and predator avoidance because it can signal the presence of an active, nearby predator (Atema and Stenzler, 1977) or indicate an otherwise sub-optimal refuge. It is assumed that natural selection has favored those animals which avoid diurnally active predators, since *Panulirus* forages only at night and since many, but not all, identified predators of *Panulirus* are diurnally active fishes. These predators include the California sheep-head (*Pimelometopon pulchrum*), the kelp bass (*Paralabrax nebulifer*), and the cabezon (*Scorpaenichthys marmoratus*), among others (Lindberg, 1955).

Of particular interest is our finding that both excised lobster thorax and abdominal muscle are repellent to live lobsters. This means that repellency cannot simply be attributed to the release of metabolites concentrated in thorax tissues. The fact that dead crab fails to influence shelter related behavior of *P. interruptus* further suggests that substances mediating both conspecific repellency and attraction may be species-specific. Such species-specific repulsion to dead conspecifics has been reported for at least two other decapods, the lobster, *Panulirus cygnus* (Hancock, 1974), and the crab, *Cancer pagurus* (Chapman and Smith, 1979). Alarm pheromones are known to be released by injured sea anemones (Howe and Sheikh, 1975), by injured gastropod snails, (Snyder, 1966; Atema and Burd, 1975; Atema and Stenzler, 1977; Stenzler and Atema, 1977), by injured sea urchins (Snyder and Snyder, 1970; Mann *et al.*, 1984), as well as by earthworms (Ressler *et al.*, 1968), insects (*e.g.*, Maschwitz, 1964; Wilson, 1971), and aquatic and terrestrial vertebrates (*e.g.*, Muller-Velten, 1966; Reutter and Pfeiffer, 1973; Muller-Schwarze *et al.*, 1984).

Our field and laboratory observations show that aggregations of *Panulirus* form overnight. Supportive evidence comes from underwater video observations conducted during July and August, 1983, at Big Fisherman Cove, Santa Catalina Island, California. Departure from the den occurred shortly after sunset (Tyre *et al.*, unpub. data), a pattern which is repeated in laboratory tests. Lobsters were also found to return to dens in greatest numbers shortly before sunrise, a result which again is in agreement with our laboratory observation that lobsters aggregate by morning but not during the initial period following darkness onset. Changes in predisposition toward aggregation could be attributed to variable rates of chemical emission, variable receptor sensitivities, or to higher order behavioral programs or hormonal control. Whether such predisposition is influenced by ambient light intensity or by a circadian rhythm cannot presently be distinguished. It has been shown for the lobsters, *Panulirus argus*, *Nephrops norvegicus*, and *Jasus novahollandiae*, that locomotory activity varies according to light intensity and to photoperiod, but such activity is also under circadian control (Sutcliffe, 1956; Fielder, 1965b; Kanciruk and Herrnkind, 1973; Arechiga and Atkinson, 1975).

Nocturnal foraging is readily initiated by *Panulirus interruptus* (Lindberg, 1955; Winget, 1969), yet this may not be the only factor motivating departure from dens and search. Shelter seeking as described in this study could, by itself, be a distinctive and separate type of search made necessary because of both long-term seasonal and short-term catastrophic events which constantly change substrate topography, thereby creating, destroying, and modifying refuges. Our field experiments using unbaited traps demonstrate that lobsters colonize novel and previously unoccupied habitats, and nocturnal den switching without associated foraging activity has been observed in *P. argus* (Herrnkind *et al.*, 1975).

We have not yet tested the hypothesis that cohabitation truly reduces vulnerability of individual lobsters to predation. There are two principal mechanisms proposed for group living that account for selective forces which could act to reduce predation, namely, (1) individuals position themselves among cohorts to reduce their own risk of being eaten (selfish herd) (Williams, 1964; Hamilton, 1971; Milinski, 1977), and (2) greater prey vigilance reduces prey response time to predatory attack (Pulliam, 1973; Treisman, 1975a; Treherne and Foster, 1981). Because *Panulirus interruptus* exhibits dominance (Roth, 1972), as well as gregariousness, in its shelter-related behavior it would seem that this animal may be useful in exploring problems of group size, geometry, and composition, as these factors affect predator detection and prey selection by predators. Such experiments are now being conducted in our laboratory.

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